# Feedforward ankle strategy of balance during quiet stance in adults

Plamen Gatev\*, Sherry Thomas, Thomas Kepple† and Mark Hallett

Human Motor Control Section, National Institute of Neurological Disorders and Stroke, NIH, Bethesda, MD 20892, USA, \*Institute of Physiology, Bulgarian Academy of Sciences, 1113 Sofia, Bulgaria and †Rehabilitation Medicine Department, Warren Grant Magnusson Clinical Center, NIH Bethesda, MD 20892, USA

(Received 22 September 1998; accepted after revision 15 October 1998)

- 1. We studied quiet stance investigating strategies for maintaining balance. Normal subjects stood with natural stance and with feet together, with eyes open or closed. Kinematic, kinetic and EMG data were evaluated and cross-correlated.
- 2. Cross-correlation analysis revealed a high, positive, zero-phased correlation between anteroposterior motions of the centre of gravity (COG) and centre of pressure (COP), head and COG, and between linear motions of the shoulder and knee in both sagittal and frontal planes. There was a moderate, negative, zero-phased correlation between the anteroposterior motion of COP and ankle angular motion.
- 3. Narrow stance width increased ankle angular motion, hip angular motion, mediolateral sway of the COG, and the correlation between linear motions of the shoulder and knee in the frontal plane. Correlations between COG and COP and linear motions of the shoulder and knee in the sagittal plane were decreased. The correlation between the hip angular sway in the sagittal and frontal planes was dependent on interaction between support and vision.
- 4. Low, significant positive correlations with time lags of the maximum of cross-correlation of 250–300 ms were found between the EMG activity of the lateral gastrocnemius muscle and anteroposterior motions of the COG and COP during normal stance. Narrow stance width decreased both correlations whereas absence of vision increased the correlation with COP.
- 5. Ankle mechanisms dominate during normal stance especially in the sagittal plane. Narrow stance width decreased the role of the ankle and increased the role of hip mechanisms in the sagittal plane, while in the frontal plane both increased.
- 6. The modulation pattern of the lateral gastrocnemius muscle suggests a central program of control of the ankle joint stiffness working to predict the loading pattern.

A major problem for human standing posture is a high centre of gravity (COG) maintained over a relatively small base of support. The body, therefore, has a high potential energy, leading to priority of equilibrium control during almost all motor tasks including quiet standing. Research on postural control has focused mainly on two types of study. One type evaluates balance with respect to external conditions. Unexpected external disturbances reveal centrally programmed stereotyped postural responses. Afferent feedback also influences posture when the initial setting is disturbed. The second type evaluates postural adjustments to anticipated internal disturbances of balance and reveals feedforward postural adjustments (for review, see Oddson, 1990; Dietz, 1992). By feedforward, we mean that the controller predicts an external input or behaves using higher-

order processing rather than simple negative feedback of a variable.

Fewer studies have dealt with the problem of maintaining balance during quiet relaxed stance. Hellebrandt (1938) introduced the concept of the stretch reflex strategy, or 'geotropic reflex' where the shift of the COG constantly stimulated stretch afferents of postural muscles that then contracted reflexively. This strategy was questioned since the angular motion at the ankle was less than necessary to elicit a stretch reflex (Kelton & Wright, 1949). Subsequent studies supported a central organization of posture that did not regulate the ankle angle or muscle length but a more global parameter such as the position of the COG (Gurfinkel et al. 1980; Dietz, 1992). Thus, the system strategy replaced the stretch reflex strategy whose role was then limited to

coping with perturbations not predicted by the ongoing central program.

Current understanding of the system strategy, however, leaves many important questions open. The first concerns the mechanism of the system strategy. It might be based on internal central commands and/or reflexive responses in terms of a stretch reflex with a co-ordinated supraspinal gain control. Fitzpatrick et al. (1992) extrapolated from their protocol of random and gentle disturbances of stance and proposed a reflexive postural control for unperturbed stance assuming there were postural reflexes with a broad range of latencies. However, Collins & De Luca (1993, 1995), in their studies of quiet stance using a 'random walk' model of the centre-of-pressure (COP) excursions, suggested that two types of postural control, 'open-loop' and 'closed-loop', coexist in the sagittal and frontal planes. The 'open-loop' postural behaviour had a fixed time of close to a second, but its mechanism remained uncertain. The 'closed-loop' control was found to be utilized over an interval longer than a second.

Studies of the postural responses to unexpected small and slow external disturbances by support translation in the anteroposterior direction found that most people reposition the COG by swaying as a flexible inverted pendulum primarily about the ankles with little hip or knee motion. This stereotyped pattern of muscle activation was called 'ankle strategy'. When responding to larger, faster displacement of support, the primary action of most people occurs at the hip resulting in active trunk rotation or the socalled 'hip strategy' (Nashner & McCollum, 1985). The choice of a postural strategy to disturbance was found to depend on the available appropriate sensory information (Nashner et al. 1989). However, biomechanical optimization models (Kuo & Zajak, 1993; Kuo, 1995) have suggested that a mixed hip-ankle strategy in the anteroposterior direction instead of a pure ankle strategy would be used to correct postural disturbances of any speed if the main objective of optimization is a minimal 'neural effort'. The prediction was based on the limited effectiveness of ankle torques to correct disturbances due to the great moment of inertia of the whole body and on the difficulties of independent control of ankle and hip postural mechanisms. The application of these models to quiet stance, however, is still far from clear.

Studies of quiet stance have suggested separate postural strategies of quiet stance for the anteroposterior and mediolateral equilibrium depending on the stance position (Day et al. 1993; Winter et al. 1996). Hip—ankle joint coupling in the frontal plane during quiet stance was found to increase with stance width implying afferent control of lateral sway (Day et al. 1993). Moreover, the postural strategies for anteroposterior and mediolateral equilibrium may use separate afferent inputs (Gatev et al. 1996). However, there is evidence for interaction between postural strategies for two equilibria in both motor (Day et al. 1993; Winter et al. 1996) and sensory aspects (Day et al. 1993; Gatev et al. 1996), and the nature of this interaction needs further clarification.

Postural sway during quiet stance is often assumed to be a resultant sum of internal noises generated in the postural control system carrying little useful information (Ishida & Imai, 1980; Fitzpatrick *et al.* 1992). This suggests that a small and slow sway as a part of the postural control during quiet stance might be important to provide updated and appropriate sensory information helpful to standing balance.

The main aim of the present work is to assess strategies of balance during quiet stance. We sought to determine the correlation between postural muscle activity and sway events. As the choice of postural strategy depends on the support and sensory conditions, we also evaluated the influences of narrow stance width and absence of vision.

# **METHODS**

#### Experimental subjects

Seven healthy male volunteers aged 24-54 years (mean,  $42\cdot3$  years) participated in the study. They ranged in height from 165 to 185 cm and weighed between 57 and 89 kg. The study was approved by the NINDS Institutional Review Board, and all subjects gave informed consent.

# Experimental set

The kinematic data were collected using the VICON system (Oxford Metrics Inc., Oxford, UK) with five CCD (charge-coupled device) cameras. The cameras were calibrated in a volume extending 2.0 m in the vertical (Z),  $1\cdot 2$  m in the anterior (Y) and  $0\cdot 6$  m in the lateral (X) direction. Camera system calibration and threedimensional target reconstruction were done by AMASS (Adtech, Adelphi, MD, USA) software. Average residual errors did not exceed 3 mm for each camera. A camera non-linearity process was performed before the camera calibration and was applied to all kinematic data. The co-ordinate system of the laboratory had a positive sense in the directions: Z = up, Y = forward, X = right. Retroreflective spherical markers covered with 3 M high gain 7610 retroreflective tape of 25.4 mm diameter were affixed bilaterally to the fifth metatarsal head, lateral malleolus, lateral femoral epicondyle, greater trochanter, acromion, cheekbone in front of the tragus, forehead, elbow, and the styloid process of the radius. Rootmean-square (RMS) noise level of the system measured at the right ankle marker did not exceed 0.2 mm for X and Z and 0.3 mm for Ycomponents.

Kinetic data were collected by a force platform AMTI type OR6-3 (Advanced Mechanical Technology, Inc., Newton, MA, USA), that measures the X, Y and Z forces (Fx, Fy and Fz) as well as the X, Y and Z moments (Mx, My and Mz). The centre of pressure (COP) (at the force transducers) was determined based on the cross product:

Moment on plates 
$$=$$
 (COP)(Force).

From this, the X (CPx) and Y (CPy) co-ordinates of the COP at the surface of the plate were determined:

$$CPx = ([(CPz)(Fx)] - My)/Fz$$

and

$$CPy = ([(CPz)(Fy)] + Mx)/Fz,$$

where CPz is the distance from transducers to the surface of the plate.

Bipolar electrodes with preamplifiers (frequency band, 10–40 kHz; gain, ×300) were fixed to the right anterior tibial, lateral

gastrocnemius, femoral quadriceps (vastus lateralis) and femoral biceps (lateral head) muscles. Two simultaneous recordings were made from each muscle with leading-off sites separated by about 3 cm along and 2 cm across the muscle fibres. The EMG signal was preamplified, then sequentially high-pass filtered, rectified and low-pass filtered with a 50 Hz Bessel filter and amplified. Video and force platform data were synchronously sampled (sampling rate, 50 Hz) with the EMG data (sampling rate, 200 Hz) by a PDP-11/73 computer (10-bit ADC) and transferred to a VAX 11/750 computer. The collected kinematic and kinetic data underwent a smoothing procedure with a second order Butterworth filter (6 Hz) with the data filtered in the forward and reverse direction to avoid phase lag (Winter, 1990).

The task of the subject was to step on the force platform after a command and to maintain balance holding a very light wooden bar (weight, 50 g; length, 0.9 m) in his hands with the arms freely hanging along the body and forearms in supination. This arm position was chosen to avoid both masking the markers and having the arms enter into the dynamics. Subjects were instructed to stand quietly.

Four experimental conditions were studied: (1) EO, standing with eyes open and natural support area (approximately 1–2 in between the heels and 10 in between the toes); (2) EC, standing with eyes closed and natural support area; (3) EOR, standing with eyes open and with feet close together (Romberg stance); and (4) ECR, standing with eyes closed and with feet close together. The duration of each whole trial was 50 s. The initial epoch of the first 13 s was discarded from the analysis. There were five trials for each condition; sufficient time for rest was allowed between the trials and between the conditions.

#### Measures and statistical procedures

Postural alignment. The right 'COG', which we will refer to as the COG, was calculated according to Dempster (1956) using the set of markers on the right side and assuming head and trunk as a whole. This procedure produces a measure to the right of the true COG. Mid-ankle point Y and X co-ordinates were calculated from the data for the two ankle markers. Quasijoint right ankle and hip angles were computed based on the relationship between markers. The trunk and pelvis were assumed as a whole for the hip angle computation.

The following were measured: (1) anteroposterior and mediolateral displacements of the COG from the mid-ankle point; (2) right ankle angle in the sagittal plane defined by foot, ankle and knee markers on the right side; (3) right hip angle in the sagittal plane defined by the knee, hip and shoulder markers; and (4) right hip angle in the frontal plane defined by the knee, hip and shoulder markers. The mean of all frames during the last 37 s of the trial was calculated and used to measure the mean of the means and s.D. for each condition and each subject.

Postural sway. Balance during the four experimental conditions was described by the following measures: (1) standard deviation (s.d.) and range of anteroposterior sway of COG during each trial (duration 37 s, sampling rate 50 Hz); (2) s.d. and range of mediolateral sway of COG; (3) s.d. and range of angular motion of the right ankle angle defined by the foot, ankle and knee markers; (4) s.d. and range of angular displacements of the right hip angle in the sagittal plane defined from knee, hip and shoulder markers; and (5) s.d. and range of angular displacements of the right hip angle in the frontal plane defined from knee, hip and shoulder markers. The mean and s.d. of each measure for each condition were calculated; s.d. is numerically equivalent to the RMS of a signal that has a mean value of zero. These measures of angular motion were chosen

to obtain data for co-ordination of body parts in addition to COG motion data.

Cross-correlation analysis. The data were subjected to correlation analysis using a program specially designed for this study to make cross-correlation between two signals (Draper & Smith, 1981). The cross-correlation window was 10 s with a maximal time shift of 3 s. The sampling interval was 80 ms (125 samples in 10 s). The sampling step of 80 ms was used because this was the largest step time that could be used without aliasing the 6 Hz signal. Using the largest step time reduced processing time and increased the value of the correlation coefficient needed for significance, thus avoiding false positives. Slow linear trends were eliminated by baseline correction for the whole cross-correlation epoch of 16 s. To remove the slow drift (or DC) component of the signal, a line was made through the first and last data points, and each data point was adjusted by the following equation:

$$Y(t)' = Y(t) - (Y(0) + (slope \times time)),$$

where Y(t)' is the adjusted value of the signal at time t, Y(t) is the original value of the signal at time t, Y(o) is the first signal value and the slope is: (Y(last) - Y(o))/sampling period. Thus, the correlation analysis focused on postural sway frequency content from 0.1 to  $6\,\mathrm{Hz}$ . Cross-correlations were done for two separate epochs for each trial; all cross-correlation functions were averaged. Cross-correlation was evaluated between: (1) anteroposterior motions of the COG and the COP; (2) EMG activity of the lateral gastrocnemius muscle and the anteroposterior motion of the COG; (3) EMG activity of the lateral gastrocnemius muscle and the anteroposterior motion of the COP; (4) EMG activity of the lateral gastrocnemius muscle and angular motion of the anatomical ankle angle defined by the foot, ankle and knee points; (5) COP anteroposterior motion and angular motion of the anatomic ankle angle defined by the foot, ankle and knee points; (6) anteroposterior motion of the COP and angular motion of the knee angle in the sagittal plane defined by the ankle, knee and hip points; (7) anteroposterior motion of the COP and angular motion of the hip angle in the sagittal plane defined by the knee, hip and shoulder points; (8) anteroposterior motions of the knee and shoulder points; (9) mediolateral motions of the knee and shoulder points; (10) anteroposterior motion of the hip point and angular displacement of the hip angle in the sagittal plane defined by the knee, hip and shoulder points; (11) mediolateral motion of the hip point and angular motion of the hip angle in the frontal plane defined by the knee, hip and shoulder points; (12) anteroposterior motion of the right head point and the COG; and (13) angular motions of the hip angle in the sagittal and frontal planes defined by the knee, hip and shoulder points.

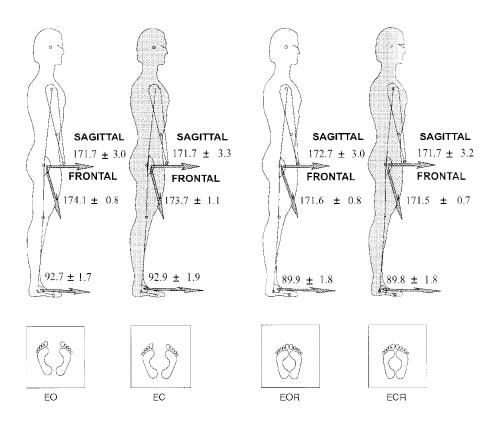
The value and time shift of the highest extremes of the averaged cross-correlation function for each condition and for each subject were measured. The correlation between the two planar projections of the hip angle was done to test the association between the anteroposterior and lateral sway or the so-called diagonal sway. Since left-to-right diagonal sway and right-to-left sway may cause a positive or negative correlation depending on the prevailing direction, we also averaged the absolute values of the crosscorrelation extremes. This will indicate a preference for diagonal sway regardless of which diagonal is preferred. The value of each maximal cross-correlation coefficient underwent Z-transformation to normalize the data (Sachs, 1982). The difference from zero of the mean maximal cross-correlation coefficient of the group for a given condition was tested by means of Student's t test. As a level of significance, P < 0.001 or Zr > 0.31 was used to prevent excessive false positives. After the statistical procedures, the Z-transformed correlation coefficients were transformed back to the correlation

coefficients that are presented in the figures for the convenience of the reader. In the time lag of the maximum of the cross-correlation function, the difference of the mean time lag of the group from zero was tested with Student's t test for each condition. A two-way ANOVA test was applied to evaluate the statistical significance of the factor width of the support with two levels: normal and narrow support (Romberg stance); and the factor of vision with two levels: eyes open and eyes closed. P < 0.05 was used as the level of significance.

# RESULTS

# Postural alignment

The means and s.d.s for the group of the postural alignment measures during the four conditions are presented in Fig. 1. The means of ankle angle for the group varied about 3 deg between the conditions and were, in general, smaller with the Romberg stance. The means of hip angle of the group in the sagittal plane showed similar values in all conditions except in EOR, when this angle was about 1 deg larger. The COG in the Y direction was closer to the mid-ankle point by 4–5 mm during narrow width stance conditions. These findings indicate a tendency for postural change with narrow stance including dorsiflexion at the ankle, extension at the hip, and movement of the COG backward. However, none of these changes reached statistical significance. The hip angle in the frontal plane decreased significantly by about 2 deg with narrow stance  $(F=11\cdot1,\ P<0\cdot05)$  reflecting decreased hip lateral flexion due to thigh



Distance of centre of gravity from ankle pivot

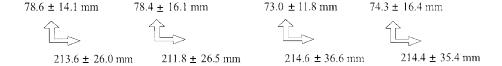


Figure 1. Postural alignment during standing with normal stance width and eyes open (EO), standing with normal stance width and eyes closed (EC); standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR)

Top, group means  $\pm$  standard error of mean (s.e.m.) (n=7) of the ankle and hip angles (all in deg) in the sagittal plane and hip angle in the frontal plane during four conditions. Bottom, group means  $\pm$  s.e.m. of the distances of the right centre of gravity (COG) to the mid-ankle point in the sagittal and frontal planes during the four conditions.

Table 1. The effects	of support and vision	n on several measure:	s of postural sway
Table 1. The checks	of support and visio	n on several measure	o or posturar sway

Parameter	Support (A)	Vision (B)	AB interaction
Centre of gravity anteroposterior sway			
S.D.	$1\cdot 2$	0.17	0.16
Range	$2 \cdot 6$	0.10	0.02
Centre of gravity mediolateral sway			
S.D.	43.9*	0.16	0.06
Range	45.2*	0.35	0.27
Ankle angle angular motion			
S.D.	17.62*	0.57	$2 \cdot 27$
Range	23.64*	3.8*	1.4
Hip angle angular motion in sagittal plan	e		
S.D.	0.03	0.37	1.02
Range	1.65	0.5	0.2
Hip angle angular motion in frontal plane	•		
S.D.	6.04*	1.01	1.94
Range	$2\cdot 4$	2.4	2.5

The tabular values are results from a two-way ANOVA. \* P < 0.05. Degrees of freedom = 1.

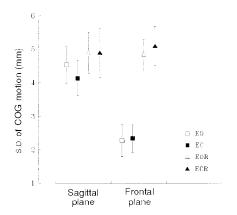
adduction (Fig. 1). There was a very small difference in the distance between the COG and the mid-ankle point in the X direction (< 2 mm) among the four conditions. ANOVA revealed no significant effect of vision, nor were there any interactions between support and vision.

# Postural sway

The mean values of the s.Ds from the COG mean position in the sagittal plane showed similar values from 4·13 to 4·90 mm during all conditions (Fig. 2); the range of sway was within narrow limits between 18 and 21 mm. s.D. and the range of motion of COG in the frontal plane was about two times smaller than that in the sagittal plane, but during narrow-based standing increased to values equal to that of

the sagittal sway. The results of ANOVA (Table 1) revealed that narrow stance led to increased mediolateral motion of COG (F = 43.9, P < 0.001 for the s.D. and F = 45.2, P < 0.001 for the range), but it was not a significant factor for the anteroposterior sway.

The group means of both s.p. and range of angular motion revealed comparable values for the ankle and hip in the sagittal plane with some predominance of hip angular motion during normal stance (Fig. 3). The within-subject variation, however, was greater for the hip than for the ankle. Angular motion at the hip in the frontal plane was about two times smaller than in the sagittal plane. ANOVA (Table 1) revealed that narrow stance led to increased ankle



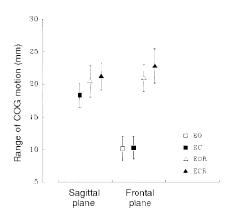


Figure 2. Centre of gravity (COG) motion in the sagittal and frontal planes during standing with normal stance width and eyes open (EO); standing with normal stance width and eyes closed (EC); standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR)

Left, group means  $\pm$  s.e.m. (n = 7) of the s.d. of the COG motion during the four conditions. Right, group means  $\pm$  s.e.m. (n = 7) of the range of the COG motion during four conditions.

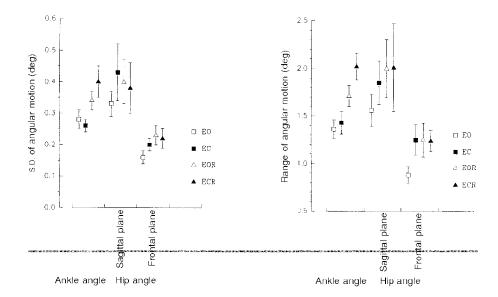


Figure 3. Angular motion of the ankle and hip angles in the sagittal and frontal planes during standing with normal stance width and eyes open (EO); standing with normal stance width and eyes closed (EC); standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR)

Left, group means  $\pm$  s.e.m. (n=7) of the s.d. of the angular motion during four conditions. Right, group means  $\pm$  s.e.m. (n=7) of the range of the angular motion during four conditions.

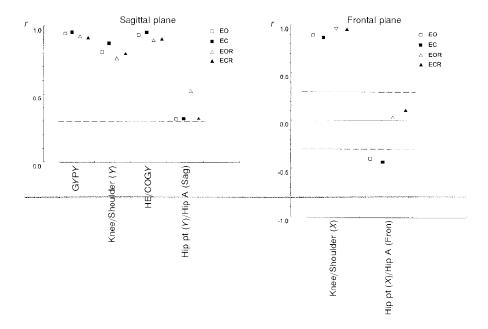


Figure 4. The correlation coefficient (r) that is a maximum or a minimum of the cross-correlation function aggregated for the whole group during standing with normal stance width and eyes open (EO); standing with normal stance width and eyes closed (EC); standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR) Left, r of cross-correlation between anteroposterior motion of centre of gravity and centre of pressure (GYPY); r of cross-correlation between the anteroposterior motion of the right knee and shoulder points (Knee/Shoulder (Y)); r of cross-correlation between the anteroposterior motion of the right hip point and angular motion of the right hip angle in the sagittal plane (Hip pt (Y)/Hip A (Sag)). Right, r of the cross-correlation between the medio-lateral (ML) motion of the right hip point and angular motion of the right hip angle in the frontal plane (Hip pt (X)/Hip A (Fron)). Lines were drawn indicating an r value of  $\pm 0.3$  at which r is different from 0 with P < 0.001.

angle sway, estimated both by the s.D.  $(F=17\cdot62, P<0\cdot001)$  and range  $(F=23\cdot64, P<0\cdot001)$ . While there was a tendency for an increased range of hip angle sway with narrow stance, there was no good evidence for increased hip motion in the sagittal plane. However, narrow stance produced a statistical increase in the s.D. of the hip angle in the frontal plane  $(F=6\cdot04, P<0\cdot05)$ .

The findings suggest that narrow stance leads to greater angular motion at the ankle, but no greater movement of the COG in the anteroposterior direction. On the other hand, with narrow stance there is both increased hip motion in the frontal plane and lateral movement of the COG. There were no significant changes due to the absence of vision nor were there any significant interactions between support and vision. Closure of the eyes in five of the subjects produced an increase of postural sway estimated by the s.D. and range of anteroposterior sway of COG and ankle angular motion, while the other two subjects showed an opposite change.

# Cross-correlation analysis

In the sagittal plane, we found high, positive maximums with zero phase of the cross-correlation between: the anteroposterior motions of COG and COP, anteroposterior motions of the right head point and the COG and the anteroposterior motions of the knee and shoulder points

(Fig. 4). The cross-correlation function between the anteroposterior motion of COP and angular motion of the anatomic ankle angle had a moderately high, zero-phased negative maximum (Fig. 5) which indicates that as the ankle extends, the COP moves backward. There was also a marginally significant, positive and zero-phased correlation between the anteroposterior motion of the hip point and angular displacement of the hip angle in the sagittal plane that became significant during narrow stance with eyes open (Fig. 4). In the frontal plane, there was a high positive correlation with zero phase between the mediolateral motions of the knee and shoulder points, and a significant, negative and zero-phased correlation of the hip point and the hip angle motions during normal stance (Fig. 4). The hip angle in both the sagittal and frontal planes showed a marginally significant correlation (absolute values) that was present only with narrow stance (Fig. 5).

A low, but significant positive correlation was found during all conditions except EOR between the EMG activity of the lateral gastrocnemius muscle and the anteroposterior motion of the COG as well as between the EMG activity of the lateral gastrocnemius muscle and the anteroposterior motion of the COP (Figs 6 and 7). These two correlations had time shifts of the maximum of cross-correlation function. The cross-correlation functions of the single trial had clearly

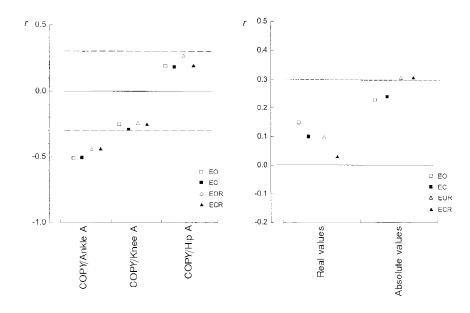


Figure 5. The correlation coefficient (r) that is the maximum of the cross-correlation function aggregated for the whole group during standing with normal stance width and eyes open (EO); standing with normal stance width and eyes closed (EC); standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR)

Left, r of the cross-correlation between the anteroposterior motion of centre of pressure and ankle angle angular motion (COP Y/Ankle A); r of the cross-correlation between the anteroposterior motion of the centre of pressure and knee angle angular motion in the sagittal plane (COP Y/Knee A); anteroposterior motion of the centre of pressure and hip angle angular motion in the sagittal plane (COP Y/Hip A). Right, r of the cross-correlation between right hip angle angular motion in the sagittal and frontal planes (real and absolute values) (Hip A (Sag)/Hip A (Fron)). Lines were drawn indicating r value of  $\pm 0.3$  at which r is different from 0 (P < 0.001).

Table 2. The effects of support and vision on the maximums of some cross-correlations

Correlations	Support (A)	Vision (B)	AB interaction	
Centre of gravity (AP sway) vs. centre of pressure (AP motion)	4.71*	0.04	0.83	
Lateral gastrocnemius muscle EMG vs. centre of gravity (AP sway)	9.26*	1.04	0.00004	
Lateral gastrocnemius muscle EMG vs. centre of pressure (AP sway)	6.77*	4.77*	1.23	
Centre of pressure (AP sway) vs. ankle angle (angular motion)	1.4	0.001	0.003	
Centre of pressure (AP motion) vs. knee angle (motion in sagittal plane)	0.26	0.41	0.05	
Centre of pressure (AP motion) vs. hip angle (motion in sagittal plane)	0.58	0.53	0.58	
Knee (Pt) vs. shoulder (Pt) (AP motions)	7.17*	2.65	0.62	
Knee (Pt) vs. shoulder (Pt) (ML motions)	10.34*	0.031	0.11	
Hip (Pt) (AP motion) vs. hip angle (angular motion in sagittal plane)	2.4	2.07	1.65	
Hip (Pt) (ML motion) vs. hip angle (motion in frontal plane)	47.88*	15.5*	44.29*	
Head (Pt) vs. centre of gravity (AP motions)	0.42	0.00006	0.35	
Hip angle (motion in sagittal plane) $vs$ . hip angle (motion in frontal plane)	0.03	0.07	0.01	

The tabular values are results from a two-way ANOVA. \* P < 0.05. Degrees of freedom = 1.

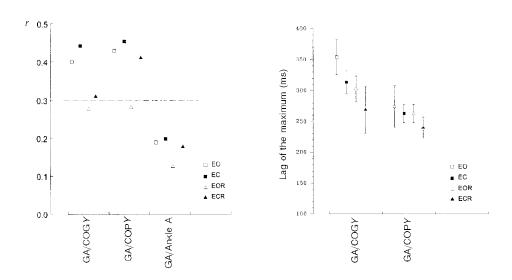


Figure 6

Left, maximum of the cross-correlation function (r) aggregated for the whole group: between the right lateral gastrocnemius muscle activity and the anteroposterior motion of the centre of gravity (GA/COG Y); between the right lateral gastrocnemius muscle activity and the anteroposterior motion of the centre of pressure (GA/COP Y); between the right lateral gastrocnemius muscle activity and ankle angle angular motion (GA/Ankle A) during standing with normal stance width and eyes open (EO); standing with normal stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR). Right, group means  $\pm$  s.e.m. (n=7) of the lag of the maximum of cross-correlation function GA/COG Y and GA/COP Y during the four conditions studied.

expressed maxima with finite time shifts in most cases (when 'r' was higher than 0·2) (Fig. 7A and C). The anteroposterior motion of the COG lagged behind EMG activity of the lateral gastrocnemius muscle in intervals ranging from 260 to 350 ms; the anteroposterior motion of the COP lagged behind EMG activity of the lateral gastrocnemius muscle in intervals ranging between 240 and 270 ms. The lag was greatest for EO and least for ECR.

There were no significant maxima of correlations between: EMG activity of the lateral gastrocnemius muscle and angular motion of the anatomical ankle angle; the anteroposterior motion of the COP and angular motion of the knee angle in the sagittal plane; and the anteroposterior motion of the COP and angular motion of the hip angle in the sagittal plane (Figs 5 and 6). There was substantial EMG activity in the other postural muscles during all trials in only a few subjects and conditions. In two subjects, there was a significant maximum of positive correlation between the femoral biceps EMG activity and anteroposterior motion of COG or anteroposterior motion of COP during all conditions, with significant lags (about 250–300 ms) for all conditions.

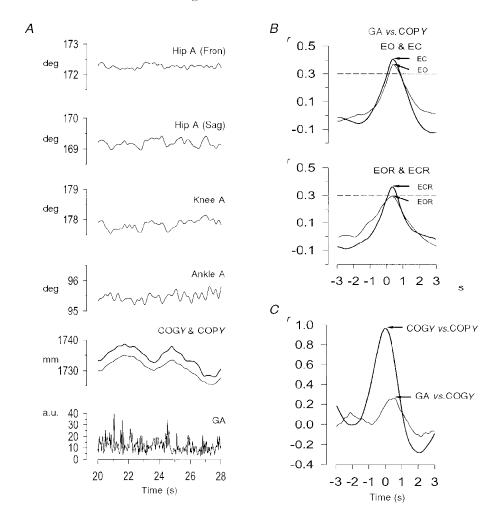


Figure 7

A, data are shown for the epoch from 20th to 28th second of a single trial in one subject during standing with normal stance width and eyes closed (EC). From bottom to top: lateral gastrocnemius muscle activity (GA), anteroposterior motion of the centre of gravity and anteroposterior motion of the centre of pressure (bold line) (COG Y & COP Y), ankle angle angular motion (Ankle A), knee angle angular motion in sagittal plane (Knee A), hip angle angular motion in sagittal plane (Hip A (Fron)). a.u., arbitrary unit. B, the cross-correlation function aggregated for the whole group between the right lateral gastrocnemius muscle activity and the anteroposterior motion of the centre of pressure (GA vs. COP Y): top, during standing with normal stance width and eyes open (EO) and standing with normal stance width and eyes closed (EC) (bold line); bottom, during standing with narrow stance width (Romberg stance) and eyes open (EOR); and standing with narrow stance width and eyes closed (ECR) (bold line). C, the cross-correlation functions for the epoch from 16th to 32nd second of the same trial (and containing the same data) shown in A: between the right lateral gastrocnemius muscle activity and the anteroposterior motion of the centre of gravity (GA vs. COG Y) and between anteroposterior motion of centre of gravity and centre of pressure (GAG Y vs. COP Y) (bold line).

ANOVA (Table 2) showed the significance of the factor support on the cross-correlations between anteroposterior motions of COG and COP (F = 4.71), between EMG activity of the lateral gastrocnemius muscle and anteroposterior motion of COG (F = 9.26) and between EMG activity of the lateral gastrocnemius muscle and anteroposterior motion of the COP (F = 6.77) (Fig. 7B). For all three, the correlation declined with narrow stance. The factor support showed significance also for the maximum of the cross-correlation function between the knee and shoulder points displacements both in the Y (F = 7.17) and X directions (F = 10.34). In the sagittal plane, the correlation declined with narrow stance, whereas in the frontal plane correlation increased. The factor of vision was significant for the maximum of cross-correlation function between the EMG activity of the lateral gastrocnemius muscle and anteroposterior motion of the COP (F = 4.77) because of increased correlation with eves closed (Fig. 7B). Vision had no effect on the maximum values of the cross-correlation function (P > 0.95) between the anteroposterior motion of COP and angular motion of the anatomic ankle angle and between the anteroposterior motions of the right head point and the COG. For the maximum of cross-correlation function between mediolateral motion of the hip point and angular motion of the hip angle in the frontal plane, both factors and their interaction were significant.

# DISCUSSION

# Ankle and hip mechanisms in quiet stance control

During normal stance we found greater angular sway around the hip in the sagittal plane compared with the sway around the ankle which is in accord with findings of Day et al. (1993). However, most of our results suggest that the ankle (plantar/dorsiflexor) mechanisms are dominant when standing with natural stance width. Only ankle angle motion correlated zero-phased with the COP excursions in the anteroposterior direction while there were no significant similar correlations of knee or hip angle. The high, positive, zero-phased correlations between the anteroposterior motions of COG and COP and between the anteroposterior motions of head and COP indicate the almost synchronous sway of the body parts. In addition, there was no significant correlation between hip linear motion and hip angle motion in the sagittal plane that would indicate the hip strategy. A possible reason for such dominance of ankle mechanisms during quiet stance instead of a mixed hip-ankle strategy suggested for disturbed stance by optimization models (Kuo & Zajak, 1993; Kuo, 1995) might be that the goal of minimal 'neural effort' during quiet stance has to be achieved through minimizing the sensory part of the effort (focusing on an increased ankle proprioceptive input, for example) rather than through its motor part.

The postural strategy of quiet stance, however, differs from the classical postural strategies that emerged from the postural disturbance studies (Nashner & MacCollum, 1985; Nashner et al. 1989; Henry et al. 1998). The postural strategy of disturbed stance is regarded as a responsive one that shifts the COG utilizing programmed triggered responses of the body with relatively fixed latencies. We found, however, that during quiet stance the EMG activity of lateral gastrocnemius muscle anticipated the anteroposterior motions of the COG and COP suggesting a predictive manner of the ankle strategy of quiet stance. That makes this strategy similar to the postural preactivation of muscles during rhythmic disturbances, when the time and magnitude of loading are expected (Dietz et al. 1993).

Narrowing the support leads to a change of the postural strategy of anteroposterior balance. The diminished correlations between anteroposterior motions of COG and COP and between the anteroposterior motions of knee and shoulder suggest a decreased role of ankle (plantar/dorsiflexor) mechanisms. The diminished correlation between EMG activity of the lateral gastrocnemius muscle and anteroposterior motions of COG or COP especially with eyes open is another feature. At the same time an increased role of hip mechanisms is illustrated by a marginal increase of hip angular motion and significant correlation between the hip point and hip angle motions during narrow stance with eyes open. Further narrowing of the stance width, i.e. during heel-to-toe stance, might lead to a dominance of hip instead of ankle mechanisms (Winter et al. 1996).

In the frontal plane during normal stance, we found a high positive correlation with zero phase between the mediolateral motions of the knee and shoulder and a significant, negative and zero-phased correlation of the hip point and the hip angle motions. These data indicate that both ankle (invertor/evertor) and hip (abductor/adductor) mechanisms control the mediolateral sway as previously found (Day et al. 1993; Winter et al. 1996).

In the frontal plane, narrowing the base led to an increased role both of ankle (invertor/evertor) and hip mechanisms suggested by the increased correlation between knee and hip mediolateral motions and the increased hip angular motion. However, the correlation of the hip point and the hip angle motions in frontal plane decreased and a marginal correlation between hip angle in both the sagittal and frontal planes appeared. This suggests that a secondary hip strategy emerges to deal with stability in both planes leading to an interaction between anteroposterior equilibrium and mediolateral equilibrium (cf. Winter et al. 1996).

Our results in both planes for the narrow stance are very similar to the findings of Winter *et al.* (1996) for standing in the 'intermediate position' in which the leading foot was 110% ahead of the rear foot and at a comfortable distance to the side. This suggests that the biomechanical constraints imposed by stance width are not the only cause of the postural strategy changeover.

# Afferent control of quiet stance

Absence of vision has only little effect on postural sway with regard to the group means. The absence of an effect of vision on postural sway has been controversial partly due to different measures of sway (for review see Oddson, 1990). A lack of effect may be due to other factors such as redundancy of sensory information and compensation by reweighting the other available sources of information. The within-subject differences in our results, however, agree with the findings of a study from two groups of healthy young individuals that integrated vision into postural control (Collins & De Luca, 1995). Absence of vision caused increased postural sway for their first group, similar to most of our subjects, whereas postural sway was unchanged for the second group. The increased correlation between gastrocnemius muscle EMG activity and anteroposterior motions of COG and COP with eye closure suggests also that individual effects of integration of vision might mask a postural mechanism based on the other senses. In addition, vestibular and/or proprioceptive senses increase when the eyes are closed (Ishida & Imai, 1980). Most probably, standing with eyes closed might better represent basic postural control mechanisms of normal stance than standing with eyes open (cf. Collins & De Luca, 1995). In line with this hypothesis is the finding that vision-independent correlations between the anteroposterior motions of head and COG might be an adaptation to the environment with different degrees of illumination. In addition, these correlations were unaffected by narrowing of the base of support as well. This permits the vestibular system to remain zero-phased in the same direction with the COG during different conditions.

During standing with narrow stance width with eyes open, the relative importance of proprioception is smallest among these conditions because of an increased vestibular sensitivity (cf. Day et al. 1993). This is consonant with the smallest values of maxima of correlation between lateral gastrocnemius muscle activity and COP or COG during this condition. However, the increase of the correlation between lateral gastrocnemius muscle activity and COP or COG with absence of vision suggests that this correlation relies heavily on proprioceptors.

The significant dependence of the correlation between the hip mediolateral motion and hip angular motion in the frontal plane on both factors of support and vision with a large interaction between them supports the hypothesis of Day et al. (1993), that hip—ankle coupling is not purely a biomechanical phenomenon, but depends also on the reweighting of the senses due to the stance width changes. A similar reweighting of senses might explain the remarkable similarity of our findings during narrow stance and the findings of Winter et al. (1996) during standing with feet in an intermediate position in which the leading foot was 110% ahead of the rear foot and at a comfortable distance to the side. Winter et al. (1996) instructed their subjects

standing with one foot on each platform to partition vertical forces to about 50% of body weight per foot with the use of visual feedback from a meter measuring both vertical signals. This task differs from the task during quiet normal stance because of the visual feedback and an increased difficulty for ankle proprioception and ankle mechanisms to deal with the required bilateral symmetry. Such a change of task might shift postural control from proprioception to vision and vestibular just like during narrow stance with eyes open. Thus, the similar features of postural strategies despite different support conditions suggests that the sensory factors have a primary importance for postural control of quiet stance.

# Feedforward and feedback mechanisms of postural control of quiet stance

The most striking finding of our study relating to the ankle strategy, was that modulation of the lateral gastrocnemius muscle activity was positively correlated with the anteroposterior motion of the COG and COP and with phase lead. Here, the correlation indicates a relationship between increased lateral gastrocnemius muscle activity and COG falling forward or, conversely, decreased muscle activity and COG going backward. Due to the position of COG in front of the ankles, its falling forward leads to increased forward bending force and loading of ankle extensors. Vice versa, COG going backward will lead to decreased forward bending force and unloading of the ankle extensors. In other words, there is a positive association between muscle activity and muscle loading. This association with a positive sense agrees with the tension-like servo control or 'climbing hill' hypothesis for balance maintenance, i.e. a muscle contracts when loaded and stays contracted until unloaded (Walsh, 1963). However, in the case of a simple servoing system, muscle activity changes are expected to respond to loading instead of being predictive of loading as indicated by our findings.

The activation of the soleus muscle before ankle movement was also seen with continuous random perturbation of posture at waist level with very gentle disturbances (200 g peak-to-peak), controlled by a weak spring (40 N m<sup>-1</sup>) to a firmly fitting belt worn around the pelvis (Fitzpatrick et al. 1992). The phase advance was frequency dependent increasing from 30 deg at 0.25 Hz to 180 deg at 5 Hz. Such phase advances are equivalent to durations of approximately 300 to 100 ms. Phase advances due to the dynamic sensitivity of the Ia afferents (Poppele & Terzuolo, 1968; Rosenthal et al. 1970; Poppele & Kennedy, 1974) and Ib afferents (Rosenthal et al. 1970) have been described. Further phase advance due to differentiation of the spinal signal in the CNS might be added to the spindle phase advance (cf. Jacks et al. 1988; Matthews, 1997). These points suggesting advancing mechanisms might explain our findings of EMG activity leading COG and COP displacements in the framework of a classical feedback model (cf. Fitzpatrick et al. 1992). However, in their more recent paper, Fitzpatrick et

al. (1996) measured loop gain of reflex feedback that is a product of reflex gain (EMG evoked per unit of movement) and the muscle and load gain (movement produced per unit of EMG). A loop gain of about unity was found that was considered by the authors to be too low to explain standing as a feedback control task. Moreover, reflex feedback control had a limited positive effect on balance, only decreasing sway by a factor of 2. In addition, the reflex feedback control was estimated to be helpful in the case of disturbances with low frequencies up to 2 Hz, but not higher. The later findings differ from the previous conclusion (Fitzpatrick et al. 1992) that reflexive feedback postural control plays a major role during disturbed stance especially when disturbing frequencies are higher than 1 Hz. As a result some feedforward control was proposed for standing balance disturbed with frequencies from 0.2 to 5 Hz (Fitzpatrick et al. 1996).

Fitzpatrick et al. (1992) found many contrasting differences between the effects of disturbances with frequencies below 1 Hz compared with those of disturbances with frequencies above 1 Hz. The disturbances below 1 Hz led to smaller coherences between the disturbance and soleus EMG, and much lower reflex gain. Nevertheless, these disturbances had more effect demonstrated by their greater influence on the ankle angle changes. Moreover, during both conditions, 'standing relaxed' and 'standing still', for the disturbances below 1 Hz the reflex gain was instruction independent, whereas the soleus EMG phase advance before the ankle movement was instruction dependent. Gain and phase showed the opposite sign of dependency on instruction when disturbances above 1 Hz were applied. These results might suggest two different kinds of postural control, the prevalence of which depends on the frequency of disturbances or different peak velocity of input at equal amplitudes (cf. Jeka et al. 1998). This interpretation agrees also with the findings of two types of postural control: 'tonic' that was immediately affected in weightlessness, and 'phasic' that was left relatively unchanged with weightlessness (Clement et al. 1984). During quiet stance the main power of internal disturbances is less than 1 Hz (Fitzpatrick et al. 1992). Thus, a clear distinction should be made between the postural control of quiet stance with steadiness as its major goal and afferent control as its major problem and the postural control of disturbed stance with a main goal of maintaining the stability of balance and facing motor rather than sensory problems.

The similarity in phase advance between central and reflexive feedback control in the low frequency range might work as an integrated system during quiet standing controlling the non-reflexive and reflexive part of ankle stiffness preparing for both internal and external disturbances. The reflexive feedback postural control probably has a minor part as suggested by Fitzpatrick et al. (1996), while central postural control plays a major part. However, our findings suggest that the central postural control of quiet stance is based on a feedforward modulation of muscle activity rather than on a

feedforward modulation of the transmission in the reflex arc. Our finding that vision affected the feedforward modulation of the gastrocnemius muscle activity contrasts with that of Fitzpatrick *et al.* (1996) who found no effect on either the reflex gain or the phase advance. The hypothesis is supported by evidence suggesting that tonic postural activity during stance is under continuous direct monitoring by the CNS (Clement *et al.* 1984) and that postural drive acts directly on the  $\alpha$  motoneurones (Ackermann *et al.* 1991).

Postural control during quiet stance may work as a twostage model of adaptive control (cf. Houk & Rymer, 1981) with motor output signals generated by two parallel processes. A 'continuous processor' works continuously to provide feedback compensation. A 'stimulus-response' (S-R) processor uses sensory cues and/or internal commands to trigger preprogrammed responses. Thus, the S-R processor can be a central mechanism controlling the descending motor commands. Adaptive control may arise mainly from a flexible S-R processor, rather than from alteration of the gain of continuous feedback loops. Postural control parameters should reflect both position and velocity of COG because of position and velocity coupling of body sway to the somatosensory drive during stance (Jeka et al. 1998). An important advantage of the central regulation included in this model is that active contraction of the muscles at the ankle joint improves perceptual acuity of proprioceptive mechanisms because it recruits primary afferents and increases firing rate of afferents already firing.

# Sway during quiet standing as exploratory behaviour; a sensory role of feedforward ankle strategy

During standing afferent input from many 'gravitydependent' receptors is required to indicate the projection of the COG within the base of support. Redundancy may be critical because it is important to know how the COG is moving in relation to the feet at all times. In addition, balance has to be maintained during different body configurations that continuously change over time (Bonnet et al. 1976). Although spontaneous sway has a lower discriminating power compared with a stimulus-response test (Ishida & Imai, 1980; Fitzpatrick et al. 1992), when extremely precise regulation of posture is necessary, one cannot passively wait for a detectable position change to trigger regulatory commands. Under these conditions, to define the spatial reference frame of the COG and to test stability of balance, small, expected sway excursions of the COG in the field of gravity may be permitted for which the system response is well defined and for which the equilibrium is not endangered. Such exploratory behaviour of quiet stance might fit the concept of the 'open-loop' postural control with a fixed time of about 1 s followed by the longer term operated 'closed-loop' postural control that returns the system to equilibrium (Collins & De Luca, 1993, 1995). The major advantage of sensory monitoring of sway is to avoid the major problem of a central program of feedforward control that would require complex models to regulate precisely a non-linear and time-varying system. Thus, central control of modulation of postural activity during standing allows continuous updating of the internal representation of stance (Clement *et al.* 1984).

# Sway restriction during quiet standing; a motor role of feedforward ankle strategy

During quiet standing, triceps surae activity is not continuous, indicating how little muscular activity is needed to maintain balance (Bonnet et al. 1976). Our finding of a correlation between postural muscle activity and COG motion as well as between COP and ankle angle motion indicates that the COG motion is permitted during standing. Thus, feedforward modulation of the muscle activity correlated with the anteroposterior motion of the COG most probably establishes the exact minimum of ankle stiffness needed to restrict the small allowable amount of sway. This strategy of postural control is possible because the low frequency of postural sway enables the fluctuating activity of the lateral gastrocnemius muscle to correlate in advance with both the viscoelastic resistance and force. Such a strategy has many potential benefits. Lengthening of an already activated gastrocnemius muscle would act in a spring-like manner to absorb body weight (Appenting & Prochazka, 1984). The compliant interface between the body and its support would also attenuate transmission of the impacts due to abrupt changes in loading to the head. In addition, feedforward setting of stiffness might avoid the residual lags in a feedback loop (Fitzpatrick et al. 1996) and subsequent deterioration of stability properties due to the tendency to oscillate (Rack, 1981). Since ankle joint stiffness depends on the moment carried by the joint (Bergmark, 1989), there is also a possibility that by leaning more or less forward, a proper level of stiffness can be chosen by adjusting the postural alignment. The choice should be based on the trade-off between the accuracy of measurement and the requirement of minimal loading or minimal expenditure of energy. This hypothesis is supported by the finding of forward body inclination during spaceflight (Clement et al. 1984) when significant diminution of loading of ankle extensors challenged load estimation and measurement. We also found a tendency for such a load-seeking behaviour with the COG situated further forward from the mid-ankle during normal stance compared with narrow stance.

- Ackerman, H., Scholz, E., Koeler, W. & Dichgans, J. (1991). Influence of postural and voluntary background contraction upon compound muscle action potentials from anterior tibial and soleus muscle following transcranial magnetic stimulation. *Electro-encephalography and Clinical Neurophysiology* 81, 71–80.
- APPENTENG, K. & PROCHAZKA, A. (1984). Tendon organ firing during active lengthening in awake, normally behaving cats. *Journal of Physiology* **353**, 81–92.
- Bergmark, A. (1989). Stability of the lumbar spine. A study in mechanical engineering. *Acta Orthopaedica Scandinavica* **60**, suppl. 30, 1–52.

- Bonnet, M., Gurfinkel, S., Lipshits, M.-J. & Popov, K. E. (1976). Central programming of lower limb muscular activity in the standing man. *Agressologie* 17 Specno, 35–42.
- CLEMENT, G., GURFINKEL, V. S., LESTIENNE, F., LIPSHITS, M. I. & POPOV, K. E. (1984). Adaptation of postural control to weightlessness. Experimental Brain Research 57, 61-72.
- Collins, J. J. & De Luca, C. J. (1993). Open-loop and closed loop control of posture: a random-walk analysis of center-of-pressure trajectories. *Experimental Brain Research* 95, 308–318.
- Collins, J. J. & De Luca, C. J. (1995). The effects of visual input on open loop and closed loop postural control mechanisms. Experimental Brain Research 103, 151–163.
- DAY, B. L., STEIGER, M. J., THOMSON, P. D. & MARSDEN, C. D. (1993).
  Effect of vision and stance width on human body motion when standing: implications for afferent control of lateral sway. *Journal of Physiology* 469, 479–499.
- Dempster, W. T. (1956). Space requirements of the seated operator: geometrical, kinematic and mechanical aspects of the body, with special reference to the limbs. Wright Air Development Center Technical Report 55-159, 1–241.
- Dietz, V. (1992). Human neuronal control of automatic functional movements: Interaction between central programs and afferent input. *Physiological Reviews* 72, 33–69.
- DIETZ, V., TRIPPEL, M., IBRAHIM, I. K. & BERGER, W. (1993). Human stance on a sinusoidally translating platform: balance control by feedforward and feedback mechanisms. *Experimental Brain Research* **93**, 352–362.
- Draper, N. & Smith, H. (1981). Applied Regression Analysis. John Wiley & Sons, Inc., New York.
- EKLUND, G. (1972). General features of vibration-induced effects on balance. *Upsala Journal of Medical Sciences* **78**, 65–72.
- FITZPATRICK, R. C., BURKE, D. & GANDEVIA, S. C. (1996). Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. *Journal of Neurophysiology* **76**, 3994–4008.
- FITZPATRICK, R. C., GORMAN, R. B., BURKE, D. & GANDEVIA, S. C. (1992). Postural proprioceptive reflexes in standing human subjects: bandwidth of response and transmission characteristics. *Journal of Physiology* 458, 69–83.
- Fung, J. & Macpherson, J. M. (1995). Determinants of postural orientation in quadrupedal stance. *Journal of Neuroscience* 15, 1121–1131.
- GATEV, P., THOMAS, S., LOU, J. S., LIM, M. & HALLETT, M. (1996). Effects of diminished and conflicting sensory information on balance in patients with cerebellar deficits. *Movement Disorders* 11, 654–664.
- Gurfinkel, V. S., Lipshits, M. I., Mori, S. & Popov, K. E. (1980). Stabilization of body position as the main task of postural regulation. *Fiziologia Cheloveka* **73**, 400–410.
- Hellebrandt, F. A. (1938). Standing as a geotropic reflex. The mechanism of the asynchronous rotation of motor units. *American Journal of Physiology* **121**, 471–474.
- HENRY, S. M., FUNG, J. & HORAK, F. B. (1998). Control of stance during lateral and A/P surface translations. *IEEE Transactions in Rehabilitation Engineering* 6, 32–42
- Houk, J. C. & Rymer, W. Z. (1981). Neural control of muscle length and tension. In *Handbook of Physiology*, vol. II, *Motor Control*, part 1, ed. Brookhart, J. M. & Mountcastle, V. B., pp. 257–323. American Physiological Society, Bethesda, MD, USA.
- ISHIDA, A. & IMAI, S. (1980). Responses of the posture-control system to pseudorandom acceleration disturbances. *Medical and Biological Engineering and Computing* 18, 433–438.

- Jacks, A., Prochazka, A. & Trend, P. St J. (1988). Instability in human forearm movements studied with feed-back controlled electrical stimulation of muscles. *Journal of Physiology* 402, 443–461.
- Jeka, J., Oie, K., Schoner, G., Dijkstra, T. & Henson, E. (1998). Position and velocity coupling of postural sway to somatosensory drive. *Journal of Neurophysiology* 79, 1661–1674.
- Kelton, I. W. & Wright, R. D. (1949). The mechanism of easy standing by man. Australian Journal of Experimental Biology and Medicine 27, 505–516.
- Kuo, A. D. (1995). An optimal control model for analyzing human postural balance. *IEEE Transactions on Biomedical Engineering* 42, 87–101.
- Kuo, A. D. & Zajac, F. E. (1993). Human standing posture: multijoint movement strategies based on biomechanical constraints. *Progress in Brain Research* 97, 349–358.
- MATTEWS, P. B. C. (1997). Spindle and motoneuronal contributions to the phase advance of the human stretch reflex and the reduction of tremor. *Journal of Physiology* 498, 249–275.
- Nashner, L. M. & McCollum, G. (1985). The organization of human postural movements: A formal basis and experimental synthesis. *Behavioral Brain Sciences* 8, 135–172.
- NASHNER, L. M., SHUPERT, C. L., HORAK, F. B. & BLACK, F. O. (1989).
  Organization of posture controls: an analysis of sensory and mechanical constraints. *Progress in Brain Research* 80, 411–418.
- Oddson, L. (1990). Control of voluntary trunk movements in man. Acta Physiologica Scandinavica 140, suppl. 595, 1–60.
- POPPELE, R. E. & KENNEDY, W. R. (1974). Comparison between behaviour of human and cat muscle spindles recorded *in vitro*. *Brain Research* **75**, 316–319.
- Poppele, R. E. & Terzuolo, C. A. (1968). Myotatic reflex: its input—output relation. *Science* **159**, 743–745.
- Rack, P. M. H. (1981). Limitations of somatosensory feedback in control of posture and movement. In *Handbook of Physiology*, vol. II, *Motor Control*, part 1, ed. Brookhart, J. M. & Mountcastle, V. B., pp. 229–256. American Physiological Society, Bethesda, MD, USA.
- Rosenthal, N. P., McKean, T. A., Roberts, W. J. & Terzuolo, C. A. (1970). Frequency analysis of stretch reflex and its main subsystems in triceps surae muscles of the cat. *Journal of Neurophysiology* **34**, 620–634.
- Sachs, L. (1982). Applied Statistics. Springer-Verlag, New York.
- Walsh, E. G. (1963). Possible factors in postural sway. In *Cerebellum*, *Posture and Cerebral Palsy*, ed. Walsh, E. G., pp. 31–37. Little Club Clinics N.3. Heinemann, London.
- WINTER, D. (1990). Biomechanics and Motor Control of Human Movement, pp. 36-41. John Wiley & Sons, Inc., New York.
- Winter, D., Prince, F., Frank, J. S., Powell, C. & Zabjek, K. F. (1996). Unified theory regarding A/P and M/L balance in quiet stance. *Journal of Neurophysiology* 75, 2334–2343.

#### Acknowledgements

P.G. was a recipient of a Central and Eastern Europe Senior Fellowship in the Neurosciences from the Fogarty Foundation, National Institutes of Health, Bethesda, MD, USA.

### Corresponding author

M. Hallett: Clinical Director, NINDS, National Institutes of Health, Building 10, Room 5N-226, 10 CENTER DR MSC 1428, Bethesda, MD 20892-1428, USA.

Email: hallett@codon.nih.gov